MOVEMENTS, CONNECTIVITY, AND RESOURCE SELECTION OF ROCKY MOUNTAIN BIGHORN SHEEP

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Species that exist in naturally fragmented subpopulations can maintain long-term viability through inter-population connectivity and recolonization of suitable habitat. We used radiotelemetry to study movements of 3 herds of bighorn sheep (*Ovis canadensis*) that recently colonized previously unoccupied parts of western Montana. These herds also provided a unique opportunity to compare resource-selection patterns in newly colonized habitats, and we used logistic regression in a global information system framework to generate predictive models for females in each herd. We detected relatively long (19- to 33-km) extra–home range movements by males in all 3 herds, and connectivity with nearby bighorn and domestic sheep herds. An information-theoretic approach to model selection revealed greater differences in resource selection among herds than anticipated. Initial evaluation of resource-selection models by resubstituting data showed excellent predictive accuracy ($P \leq 0.002$), but testing models across sites gave mixed results, and in many cases, poor fit ($0.001 \leq P \leq 0.960$). High vagility of males and variability in resource selection by females suggests increased potential for future recolonization and connectivity.

Key words: bighorn sheep, connectivity, habitat, movement, *Ovis canadensis*, resource selection

Species with specialized habitat requirements often are segregated into disjunct subpopulations because of both natural and anthropogenic fragmentation of suitable habitat. In the spectrum of large herbivores, bighorn sheep (*Ovis canadensis*) provide a good example of such a species (Bleich et al. 1990; DeForge et al. 1979). Unlike other North American ungulate species, bighorn sheep have not fully recovered from dramatic population declines during the 19th century. After the extinction of 1 subspecies (*O. c. auduboni*) and local extirpations in several states, restoration efforts brought population estimates in the contiguous United States to 49,000 in 1991 (Valdez and Krausman 1999). Although overall numbers are improving, local populations remain fragmented and small (Douglas and Leslie 1999), with the majority at numbers far below minimum viable population estimates (Berger 1990; Krausman et al. 1992; Lande 1995).

Habitat specialists are typically poor colonizers (MacArthur and Wilson 1967) and sheep have been perceived as such, with strong site fidelity (Geist 1970, 1971; Shackleton et al. 1999).

Thus, costly reintroductions and supplemental transplants have been a primary tool in augmenting populations during recent decades (Hansen 1980). Shackleton et al. (1999) suggested that anthropogenic changes to the landscape have forced this species into more specialized habitats than previously occupied. In addition, bighorn sheep may have a greater capacity for extra–home range or dispersal movements than previously envisioned (Bleich et al. 1996; Festa-Bianchet 1986b; Schwartz et al. 1986). Schwartz et al. (1986) reviewed a host of studies noting intermountain movements of desert bighorn (*O. c. nelsoni*) males and females across highways and rivers, and Bleich et al. (1996) used mitochondrial DNA to reveal metapopulation dynamics of desert bighorn populations within 15 km of one another. Interpopulation movements of Rocky Mountain bighorn sheep (*O. c. canadensis*) in northern ecosystems are less well documented. Festa-Bianchet (1986b) documented males up to 48 km from the site of their capture in southern Alberta, and Singer et al. (2000a) monitored 24 cases of dispersal of translocated Rocky Mountain bighorn sheep from release patches to neighboring unoccupied patches. Although movements of this type can enable gene flow and rescue effects, they also may serve as a disease vector, to which bighorn populations have proven very vulnerable (Bunch et al. 1999; DeForge et al. 1979; Fitzsimmons et al. 1995; Sausman 1984). As a result, issues of habitat quality (Johnson and Swift

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2000; Turner et al. 2004), connectivity (Krausman 1997; Singer et al. 2000b), and disease (Gross et al. 2000) all play a role in the viability of each local population.

Existing bighorn populations in western Montana include native and reintroduced lineages (McCarthy 1996). During the 1980s bighorn sheep colonized 3 previously unoccupied areas of western Montana. We radiotracked animals from these young herds to study movements and connectivity in a northern landscape occupied by both native bighorn and domestic sheep. These populations also provided a unique opportunity for studying the degree of similarity in resource selection at newly pioneered habitats. We developed and evaluated resource-selection functions for each herd, and compared and rigorously tested all models with independent data from the other 2 herds, as recommended by Verbyla and Litvaitis (1989), Fielding and Bell (1997), and Boyce et al. (2002). We quantitatively asked whether recolonized populations selected resources similarly, and assessed the effectiveness of applying site-specific models across areas.

MATERIALS AND METHODS

Study area.—We studied 3 newly colonized bighorn sheep populations (Bearmouth, Garrison, and Skalkaho) in the Rocky Mountains of western Montana at elevations of roughly 1,100–2,000 m. The Bearmouth (46°43′N, 113°27′W) herd occupied parts of the southern Garnet Range, 50 km east of Missoula, Montana, and numbered approximately 12–17 individuals during the study period (DeCesare 2002). The Garrison (46°31′N, 112°50′W) herd was located in the northeastern foothills of the Flint Creek Range, 100 km east of Missoula, and contained an estimated 55–74 individuals (DeCesare 2002). The Skalkaho (46°10′N, 113°59′W) herd was in the western Sapphire Mountains, 75 km south of Missoula, and consisted of roughly 58–62 individuals (DeCesare 2002). Each site was roughly 70 km from the other 2 sites, and other bighorn herds existed in between.

All 3 herds occupied low- to midelevation habitats where common native grassland species included bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and rough fescue (*Festuca scabrella*). Shrub species included sagebrush (*Artemesia tridentata*) and mountain mahogany (*Cercocarpus ledifolius*), and forests were dominated by open stands of ponderosa pine (*Pinus ponderosa*) and denser stands of Douglas-fir (*Pseudotsuga menziesii*). Exotic species such as cheatgrass (*Bromus tectorum*) and spotted knapweed (*Centaurea maculosa*) also were common.

Capture and monitoring.—We captured 16 adult female and 5 adult male bighorn sheep at 3 sites in March 2001, using a net-gun fired from a helicopter (Krausman et al. 1985) and fitted all animals with Telonics MOD-500 VHF radiocollars (Telonics, Mesa, Arizona). We attempted to capture animals from different subgroups within each herd and radiocollared 2, 7, and 7 females in Bearmouth, Garrison, and Skalkaho herds, respectively. Although males were valuable for movement studies, small sample sizes of radiocollared males ($n = 2, 2,$ and 1, respectively) prevented inclusion of male data in resource-selection analysis. We used primarily ground radiotelemetry to collect 1,034 locations for collared females and 219 for males between March 2001 and August 2002. All handling and monitoring of animals followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and were approved by an institutional animal care and use committee.

Movements.—We quantified movements in reference to home ranges of resident females. We calculated 5% fixed kernel estimates

TABLE 1.—Descriptions of variables derived from a global information system to quantify resource selection of bighorn sheep, western Montana, 2001–2002.

Variable	Description
ELEV	Elevation (m)
SLOP	Slope (degrees)
ASPECT[a]	Slope aspect, treated as 3 indicator variables
SRI	Solar radiation index
DESCP	Distance to nearest escape terrain (m)
DWATR	Distance to nearest water (m)
DROAD	Distance to nearest road (m)
DGRAS	Distance to nearest xeric grass or shrubland (m)
DOPFOR	Distance to nearest open canopy forest (m)
DCLFOR	Distance to nearest closed canopy forest (m)
DBGRA	Distance to nearest burned grasslands, burned summer 2000
DLBFOR	Distance to nearest low-severity burned forest, burned summer 2000
DHBFOR	Distance to nearest high-severity burned forest, burned summer 2000

[a] Aspect was divided into 4 categories based on cardinal directions, inserted in models as 3 indicator (dummy) variables, using south as the reference category.

using the Animal Movement 2.0 Extension (Hooge and Eichenlaub 1997) for ArcView 3.2a software (ESRI, Redlands, California) and all female locations for each herd. We used the centroids of these core female home ranges as reference points for measuring movement. We measured the furthest distance traveled by each male and female from core female home ranges and documented all associations with nearby bighorn and domestic sheep herds.

Resource selection.—We maintained a minimum of 3 days between bighorn relocations to ensure temporal independence of data (McNay et al. 1994; Otis and White 1999; Swihart and Slade 1985; Swihart et al. 1988). A modified nearest-neighbor analysis of spatial independence revealed a lack of independence in relocations among individuals (DeCesare and Pletscher 2005), which can bias habitat-selection results (Dasgupta and Alldredge 2000; Millspaugh et al. 1998). Therefore, we pooled data within each herd and the sampling unit became the location of a group of sheep, which included 1 or more collared animals. Sample size was reduced from 1,034 individual female locations to 523 group locations.

Bighorn sheep generally select resources differently by season (Festa-Bianchet 1986a, 1986b; Geist 1971; Shannon et al. 1975). We divided data for each herd into 3 biologically meaningful seasons (winter, lambing, and autumn) using shifts in movements or behavior to delineate each season. Generally, the lambing season lasted from early May through late July, the autumn season from early August through late November, and the winter season from early December through late April. This division resulted in 3 sets of group locations each for the Bearmouth ($n_{winter} = 47$, $n_{lambing} = 49$, and $n_{autumn} = 20$), Garrison ($n_{winter} = 69$, $n_{lambing} = 72$, and $n_{autumn} = 51$), and Skalkaho ($n_{winter} = 95$, $n_{lambing} = 76$, and $n_{autumn} = 44$) study sites.

We selected explanatory variables for resource-selection modeling from the literature (Table 1), and compiled these data in a global information system (GIS) using ArcView 3.2a and the Spatial Analyst extension. We derived 30 × 30-m grids of elevation, slope, and aspect from the United States Geological Survey National Elevation Dataset (http://ned.usgs.gov/). We also derived a solar radiation index combining latitude, slope, and aspect that has proven a significant predictor of bighorn sheep habitat use (Dicus 2002; K. Keating, pers. comm.). We defined areas with slopes >27° as escape terrain (Andrew et al. 1999; Dunn 1996; McCarty 1993; Smith et al. 1991) and quantified

TABLE 2.—Maximum distances moved from core female home ranges and estimated ages at the time of movement for individual males and all collared females at 3 study sites in western Montana, 2001–2002.

Study site	Animal	Age (years)	Maximum distance from core female home ranges (km)
Bearmouth	Male 1	9	18.9
Bearmouth	Male 2	3	19.2
Garrison	Male 3	4	32.9
Skalkaho	Male 4	5	9.4
Skalkaho	Male 5	2	30.9
Bearmouth	Females ($n = 2$)	Adult	7.4
Skalkaho	Females ($n = 7$)	Adult	9.8
Garrison	Females ($n = 8$)	Adult	3.7

distance (m) from escape terrain patches. We created a minimum patch size for escape terrain (0.7 ha) based on the smallest patch we observed sheep using for escape. We used TIGER 2000 Census data (http://www.census.gov/geo/www/tiger/) to measure distance to water and distance to roads.

We used the SILC3 Land Cover Classification Data (Wildlife Spatial Analysis Lab, in litt.) to quantify vegetation types at 30 × 30-m resolution. We simplified cover types into 3 basic categories (xeric shrub and grassland, open canopy forest, and closed canopy forest). Two study sites experienced wildfires during summer 2000, after SILC3 data were generated. We used fire severity data (Wildlife Spatial Analysis Lab, in litt.) to edit SILC3 vegetation data and create 3 additional vegetation classes (burned grass, low-severity burned forest, and high-severity burned forest). We included these cover types in habitat-selection models as a set of 6 continuous variables by quantifying distance from locations to each cover type (Miller et al. 2000) and removing categories not biologically relevant to each study site.

Numerous bighorn habitat suitability models have highlighted horizontal visibility as a key component of bighorn habitat (Johnson and Swift 2000; Risenhoover and Bailey 1980, 1985; Smith et al. 1991; Zeigenfuss et al. 2000). We found no strong preference for areas with high horizontal visibility in separate analyses using the same study animals (DeCesare and Pletscher 2004) and did not include horizontal visibility as an explanatory variable in GIS-based modeling.

We modeled Johnson's (1980) 3rd-order selection (habitat selection within the home range) comparing habitat used by animals to that available. Female group locations provided a sample of habitats used. Definitions of available habitat are somewhat arbitrary (Aebischer et al. 1993; Wilson et al. 1998); we used a 100% minimum convex polygon with an additional 100-m buffer to approximate the area available to each herd during the study period (McCorquodale 1999). Seasonal home ranges overlapped greatly, so we used a single, year-round home range to define available habitat at each site. Three locations gathered during forays to outlying areas not considered part of the home range (Burt 1943) were removed before calculating availability minimum convex polygons. We drew a systematic sample of points ($n_{Bearmouth} = 2{,}428$, $n_{Garrison} = 1{,}204$, and $n_{Skalkaho} = 1{,}953$) from a 100 × 100-m grid within minimum convex polygons to estimate habitat availability (Erickson et al. 1998). To compensate for large and autocorrelated samples, we randomly selected 200 locations from the systematic samples to quantify availability for initial model comparisons. We then reran best models with the full samples to obtain more precise and unbiased coefficient estimates (Burnham and Anderson 1998; T. McDonald, West Inc., pers. comm.).

We used logistic regression to estimate 9 resource-selection functions (Manly et al. 2002), or 1 for each site in each season. Using logistic regression with use-availability data presents some problems; predicted values are not scaled between 0 and 1, and are not necessarily valid resource-selection probabilities (Keating and Cherry 2004; Manly et al. 2002). Instead, resource-selection functions provided an index for probability of use and a method to rank habitats selected by bighorn sheep (Keating and Cherry 2004).

We used the information-theoretic methods of model selection (Burnham and Anderson 1998) to avoid overfitting models to site-specific data. We developed 10 a priori candidate models for each season based on literature review and field observation. We fit global models with all meaningful explanatory variables and used the Hosmer and Lemeshow goodness-of-fit test to evaluate general model fit before selecting among candidate models (Burnham and Anderson 1998; Hosmer and Lemeshow 2000). We also tested for correlation among independent variables to ensure that correlations among included variables did not affect results.

We used the same set of seasonal candidate models for each site (with some variation in applicable cover type categories), and calculated the Akaike information criterion, corrected for small sample sizes (AIC$_c$), to discriminate fit and parsimony of candidate models (Burnham and Anderson 1998). We calculated differences in AIC$_c$ values (Δ_i) between the lowest-scoring model and each candidate model. When multiple models scored $\Delta_i < 2$, the best model was unclear (Burnham and Anderson 1998). Model averaging procedures based on Akaike weights (w_i) resulted in parameter-heavy and difficult-to-interpret best models. Thus, when multiple models scored $\Delta_i < 2$, we selected the model with the fewest parameters as the best model to maintain parsimony.

For initial model evaluation, we generated predictions from the same data used to create the model. This resubstitution can lead to optimistic estimates of model accuracy (Chatfield 1995; Fielding and Bell 1997; Verbyla and Litvaitis 1989), but remains a common approach to model validation. Second, we applied models across independent study sites for a more robust and unbiased validation of each model. Testing models across sites also was a means to assess how similarly females of recently colonized populations selected habitat. To evaluate the prediction success of models, we calculated the degree of correlation between predicted probabilities in a GIS landscape and the measured use of that landscape. We used a Spearman rank correlation to test for correlation between the density of use across the landscape and the predicted probability of use from each model (Boyce et al. 2002). We repeated this multiple times but did not use a Bonferroni correction (Cabin and Mitchell 2000; Garcia 2004; Moran 2003); the value of these tests was in comparing the internal and external validation of models, not generating specific probability values.

RESULTS

Movements.—Bearmouth, Garrison, and Skalkaho females remained localized within home ranges, making maximum movements of 3.7, 7.4, and 9.8 km from core female home ranges (Table 2), respectively. None of these movements overlapped with home ranges of nearby herds of bighorn or domestic sheep.

We detected relatively long extra–home range movements for males in all herds and 4 of 5 collared animals (Table 2). These movements occurred primarily during summer months (May–September) but 1 male continued moving back and forth

TABLE 3.—Candidate models and selection criteria for information-theoretic model for bighorn sheep selection at 3 study sites and seasons in western Montana, 2001–2002. Best models, selected as those with the fewest variables when $\Delta_i < 2$, are in bold type. Variables used in models are defined in Table 1.[a]

		Study sites									
		Bearmouth				Garrison				Skalkaho	
Candidate models per season	k	AIC_c	Δ_i	w_i	k	AIC_c	Δ_i	w_i	k	AIC_c	Δ_i	w_i
Winter												
ELEV	2	218.33	27.31	0.00	2	310.29	60.71	0.00	2	354.48	104.36	0.00
SLOP, ASPECT	5	224.19	33.17	0.00	5	311.97	62.39	0.00	5	354.20	104.08	0.00
ELEV, SLOP, SRI	4	200.16	9.14	0.00	4	274.63	25.05	0.00	4	351.47	101.35	0.00
ELEV, SLOP, SRI, DESCP	5	202.17	11.15	0.00	5	258.56	8.98	0.00	5	349.40	99.28	0.00
SLOP, SRI, DESCP, COVTYP	9	191.11	0.08	0.32	6	287.71	38.13	0.00	10	251.66	1.54	0.23
ELEV, SLOP, DESCP, COVTYP	9	193.70	2.67	0.09	**6**	**250.10**	**0.52**	**0.33**	10	255.41	5.29	0.04
SRI, DESCP, COVTYP	**8**	**191.02**	**0.00**	**0.33**	5	290.79	41.21	0.00	**9**	**250.12**	**0.00**	**0.51**
ELEV, SLOP, SRI, DESCP, COVTYP	10	191.61	0.59	0.25	7	250.74	1.16	0.24	11	252.84	2.72	0.13
SLOP, SRI, DESCP, DROAD	5	202.35	11.32	0.00	5	309.05	59.47	0.00	5	341.87	91.75	0.00
ELEV, SLOP, ASPECT, DESCP, COVTYP	12	197.84	6.81	0.01	9	249.58	0.00	0.43	13	253.47	3.35	0.09
Lambing												
SLOP, DESCP	3	224.42	8.04	0.00	3	259.00	109.32	0.00	3	289.76	85.23	0.00
SLOP, SRI, DESCP	4	222.37	5.98	0.01	4	258.31	108.63	0.00	4	257.65	53.12	0.00
SLOP, ASPECT, DESCP, DWATR	7	218.64	2.25	0.08	7	239.73	90.04	0.00	7	263.59	59.07	0.00
ELEV, SLOP, DESCP, DROAD	5	226.25	9.86	0.00	**5**	**149.69**	**0.00**	**1.00**	5	291.06	86.54	0.00
ELEV, SLOP, SRI, DESCP	5	224.36	7.98	0.00	5	202.35	52.67	0.00	5	258.92	54.40	0.00
ELEV, SLOP, SRI, DESCP, COVTYP	10	218.54	2.16	0.09	7	204.36	54.67	0.00	11	207.41	2.88	0.19
ELEV, SLOP, DESCP, COVTYP	9	216.44	0.05	0.25	6	203.45	53.76	0.00	10	213.59	9.07	0.01
ELEV, SLOP, SRI, DESCP, DWATR	6	217.01	0.62	0.19	6	171.05	21.36	0.00	6	247.19	42.66	0.00
SLOP, DESCP, DWATR	**4**	**218.25**	**1.86**	**0.10**	4	244.66	94.98	0.00	4	289.07	84.55	0.00
ELEV, SLOP, SRI, DESCP, DWATR, COVTYP	11	216.39	0.00	0.26	8	167.28	17.59	0.00	**12**	**204.52**	**0.00**	**0.80**
Autumn												
SLOP, DESCP, COVTYP	8	130.91	0.68	0.14	5	237.53	49.52	0.00	**9**	**182.24**	**0.00**	**0.31**
ELEV, SLOP, SRI, DESCP, COVTYP	10	131.48	1.24	0.10	7	191.04	3.03	0.10	11	185.90	3.66	0.05
ELEV, SLOP, SRI, DESCP	5	132.46	2.23	0.06	5	188.57	0.56	0.35	5	232.87	50.63	0.00
ELEV, SLOP	**3**	**131.16**	**0.92**	**0.12**	3	206.57	18.56	0.00	3	229.62	47.39	0.00
ELEV, SLOP, DESCP	4	131.53	1.29	0.10	**4**	**188.01**	**0.00**	**0.46**	4	230.94	48.70	0.00
SLOP, ASPECT, COVTYP	10	135.20	4.97	0.02	7	242.57	54.56	0.00	11	184.46	2.22	0.10
ELEV, SLOP, SRI, DWATR, COVTYP	10	131.89	1.66	0.08	7	213.67	25.66	0.00	11	185.51	3.27	0.06
SRI, DESCP, COVTYP	8	130.23	0.00	0.19	5	245.88	57.87	0.00	9	182.25	0.01	0.31
ELEV, SLOP, DESCP, COVTYP	9	130.38	0.15	0.18	6	191.13	3.12	0.10	10	183.78	1.54	0.14
SLOP, ASPECT, DESCP	11	135.76	5.53	0.01	8	241.59	53.59	0.00	12	186.59	4.36	0.03

[a] k = the number of parameters; AIC_c = Akaike information criterion corrected for small sample sizes; Δ_i = differences in AIC_c values; w_i = Akaike weight; COVTYP = the set of up to 6 variables describing the distance to each vegetative cover type available at a given study area.

between core female home ranges and neighboring herd home ranges during October and December as well. The longest movement was 32.9 km from the core female home range, and 2 individuals crossed interstate I-90 and the Clark Fork River a total of 7 times. We found direct association with bighorn sheep in neighboring populations in 2 of 3 herds (3 of 5 animals) and found direct association with domestic sheep in the same 2 herds (2 of 5 animals).

Resource selection.—We found both similarities and differences in best models across seasons and study sites. The same candidate models (with differences in included cover type categories) were used for each site, but in only 1 of 9 cases were the same "best" models chosen between 2 sites (Table 3). Increasing slopes and decreasing distances to escape terrain were important explanatory variables in most cases (Table 4). Although distance to water was a significant explanatory variable in 2 of the 3 lambing models, the sign of the

coefficient revealed that females during the lambing period were actually further from water than expected. The solar radiation index proved a valuable explanatory variable in several cases, while aspect was not in a single "best" model.

Models performed well when applied to the site where they were fit ($P \leq 0.002$; Table 5), which indicated that "best" models were reliable estimates of habitat selection for given sites and seasons. Applying models to independent data from different study sites produced mixed results ($P = 0.001–0.960$; Table 5); we excluded Bearmouth autumn data from model comparisons because of low sample sizes. Although some models did quite well at predicting use at other sites, this was not consistent.

DISCUSSION

Movements.—We found that females exhibited strong fidelity to home ranges. This was consistent with past findings

TABLE 4.—Variables and coefficients included in season and site-specific best models for bighorn sheep resource selection at 3 sites in western Montana, 2001–2002. Variables used in models are defined in Table 1.

Season	Site	ELEV	SLOP	SRI	DESCP	DWATR	DROAD	DGRAS	DOPFOR	DCLFOR	DBGRA	DLBFOR	DHBFOR
Winter	Bearmouth			1.665	−0.016			−0.002		−0.003	−0.010	0.007	−0.0003
	Garrison	0.015	0.036		−0.003			−0.0003		0.004			
	Skalkaho			1.860	−0.002			−0.003	−0.001	0.006	−0.003	0.005	−0.002
Lambing	Bearmouth		0.042		−0.017	0.001							
	Garrison	0.008	0.040		−0.006		0.003						
	Skalkaho	0.001	0.077	3.001	−0.007	0.003		−0.008	−0.003	0.005	0.002	−0.005	−0.0002
Autumn	Bearmouth	−0.0002	0.0940										
	Garrison	0.0209	0.0726		−0.0027								
	Skalkaho		0.0146		−0.0002			0.0039	−0.0009	0.0050	−0.0004	−0.0004	−0.0004

(Geist 1971) and suggested that these populations represented colonizations of new habitat rather than range expansions from existing populations.

Bleich et al. (1996) defined a metapopulation of desert bighorn sheep as a set of subpopulations occupying mountain ranges less than 15 km apart, based on genetic evidence that metapopulations defined as such had unique haplotypes from one another. We observed movements of 18.9–32.9 km from core female home ranges in 4 of 5 collared males. Although the majority of these movements were not during the breeding season, these results suggest that Rocky Mountain bighorn sheep may be able to maintain genetic connectivity among subpopulations at distances greater than observed by Bleich et al. (1996) for desert subspecies. Genetic techniques similar to those used by Bleich et al. (1996) could be used to derive an alternate distance, but considerable translocations of bighorns in and out of most of western Montana's populations might blur genetic distinctions that once existed across the region (McCarthy 1996).

Our small sample of marked males ($n = 5$) also revealed a high degree of connectivity between bighorn and domestic sheep populations. Thus, we cautiously suggest that distinct populations of Rocky Mountain bighorn sheep may be more connected than previously known. If so, connectivity can create an efficient path for disease spread. We encourage further research on metapopulation dynamics of this species in northern ecosystems, because it remains unclear whether connectivity among populations serves as a genetic boost or a disease-laden liability.

Resource selection.—Females of these 3 recently colonized herds were different in their selection patterns as evidenced by our model selection and validation results. Although the presence of steep, escape terrain was consistent across sites, large differences among sites may be indicative of a lower degree of habitat specialization than commonly expected. When combined with increasing knowledge about dispersal and colonization abilities (Singer et al. 2000a; this study), these results suggest that the potential for natural recolonization of the West may be higher than previously expected.

We used resource-selection modeling to compare 3rd-order selection (Johnson 1980) within herd home ranges, and we encourage future research on 2nd-order selection, or selection of herd home ranges within larger landscapes. Singer et al. (2000a) modeled the probability of colonization for different habitat patches after sheep transplants and found that population growth rates in source herds and vegetation characteristics in corridors between source and colonized patches were predictive parameters. A resource-selection function analysis of the habitat characteristics of colonized and uncolonized patches themselves (instead of the corridor habitat) would be valuable for future habitat modeling and conservation.

All habitat-selection analyses fall under the broad assumption that selection equates with better habitat quality and population fitness (Garshellis 2000; Van Horne 1983). Comparing successful and unsuccessful reintroductions addresses this problem and could be further explored (Johnson and Swift 2000). Incorporating fitness into measures of habitat quality should be a goal for all studies of wildlife and habitat, but funding and logistics make data collection problematic.

In agreement with past bighorn sheep habitat studies (Geist 1971; McCarty and Bailey 1994; Tilton and Willard 1982) and modeling (Dicus 2002; Hughes 1997; Johnson and Swift 2000; Sweanor et al. 1996), we found slope and distance to escape terrain were important habitat variables across seasons and sites. These parameters appear universally important to bighorn sheep habitat in our study areas. However, these were not the only parameters that explained variation in resource selection, and more site-specific variation occurred in other parameters.

Distance to cover type variables revealed differences among sites. The presence of recently burned grasslands and forest

TABLE 5.—Spearman rank correlations (R values) and associated P values testing correlation between season- and site-specific resource-selection model predictions and relocation data for bighorn sheep at 3 sites, 2001–2002. Values in bold represent unbiased tests of models with independent data from other sites. We did not include the Bearmouth autumn model because of small sample size of locations.

		Model test site					
		Bearmouth		Garrison		Skalkaho	
Season	Origin of model	R	P	R	P	R	P
Winter	Bearmouth	0.879	0.001	**−0.200**	**0.580**	**0.842**	**0.002**
	Garrison	**−0.212**	**0.556**	0.964	<0.001	**−0.030**	**0.934**
	Skalkaho	**0.442**	**0.200**	**0.879**	**0.001**	0.927	<0.001
Lambing	Bearmouth	0.927	<0.001	**0.927**	**<0.001**	**0.915**	**<0.001**
	Garrison	**0.358**	**0.310**	0.976	<0.001	**−0.152**	**0.676**
	Skalkaho	**0.176**	**0.627**	**0.418**	**0.229**	0.988	<0.001
Autumn	Garrison			0.964	<0.001	**−0.115**	**0.751**
	Skalkaho			**−0.018**	**0.960**	0.855	0.002

only in Bearmouth and Skalkaho created obvious site-specific differences. Best models often included these cover type variables and sheep were likely responding to effects of the fires. Areas in or near high-visibility habitats such as grasslands and high-severity burned forests were generally preferred and low-visibility denser forests avoided. However, we did not detect selection based on horizontal visibility alone (DeCesare and Pletscher 2004) and are hesitant to associate selection of cover types to horizontal visibility. We hypothesize that horizontal visibility may be more important at the 2nd-order scale of selection (Johnson 1980) for these herds, and that within the home range, other parameters are more important. We were unable to include all potential variables in our analysis. Other factors such as predator densities, food quality, and forage abundance also may be important.

Many recent efforts identifying and modeling suitable bighorn habitat (Hughes 1997; Johnson and Swift 2000; Zeigenfuss et al. 2000) are based on the habitat-evaluation procedure of Smith et al. (1991). The habitat-evaluation procedure of Smith et al. (1991) was a stepwise procedure that identified core habitat based on escape terrain patches and subsequently removed areas from this core habitat that were unsuitable for other reasons (e.g., dense vegetation, close proximity to human development, close proximity to domestic sheep, high elk or cattle concentrations, etc.). Zeigenfuss et al. (2000) identified the 5 key habitat criteria upon which this habitat-evaluation procedure was based: close proximity to large patches of escape terrain, close proximity to water, lack of highway or water barriers, high horizontal visibility, and minimum of 150 m from human development. The importance of slope and distance to escape terrain in our models reaffirms the consideration of these variables when identifying core bighorn sheep habitat. Surface sources of water have been shown to be seasonally important to desert bighorn sheep (Bleich et al. 1997; Leslie and Douglas 1979; Turner and Weaver 1980), but this relationship is less clear for the Rocky Mountain subspecies (Shackleton et al. 1999). We found no consistent relationships between bighorn use and proximity to water, although in 2 of 3 lambing models females were actually further from water than random expectation. This result may be an artifact of high water availability in the home range relative to lambing areas, or of avoidance of dense, riparian habitats commonly associated with water in our study areas. Comparison to the habitat-evaluation procedures of Zeigenfuss et al. (2000) and other such procedures is difficult because of differences in selection scale. Most bighorn sheep habitat-evaluation procedures are developed to identify suitable bighorn home ranges within larger landscapes (Johnson's [1980] 2nd-order selection), whereas our models reflect 3rd-order selection within home ranges. We found that horizontal visibility (DeCesare and Pletscher 2004) and proximity to water and roads were not consistent factors in habitat selection within home ranges, but we cannot assess how these variables affected selection of home ranges within the larger landscape.

Dicus (2002) used similar logistic regression procedures to assess 3rd-order winter habitat selection by bighorn sheep in northwestern Montana. Parameters in his best winter range

model were slope, distance to escape terrain, solar radiation index, snow cover, and values of cover types. These parameters were similar to those we found important in our study areas and were measured at similar scales, but signs and magnitudes of coefficients were not consistent with our models. Model validation procedures such as those in this paper would provide a clearer comparison of resource selection across study sites.

Validating resource-selection functions with resubstituted data resulted in high prediction success. Had this study been limited to any 1 of these 3 sites, as is often the case, we might have been overly confident in our models' validity. The danger of applying such models to new landscapes is evident by our between-site comparisons. Although some models predicted bighorn sheep use in new areas well, site-specific variation can strongly affect their external validity. These modeling procedures elucidated differences in selection patterns across recently colonized habitats, and we encourage future use of such techniques both to compare selection across sites and to externally validate local models.

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